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BAT RESPONSES TO ARIDITY

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Bat responses to aridity

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ACADEMIC DISSERTATION

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LIST OF ORIGINAL PUBLICATIONS

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ABSTRACT

Due to the perceived low biodiversity of arid environments, species inhabiting these regions have received less research compared to tropical areas and biodiversity hotspots. However, arid conditions are predicted to characterise a larger number of regions globally and there is a greater need to identify strategies that allow species to survive in these harsh environments. Bats occupy a wide variety of habitats, including some of the most arid habitats on Earth, thanks also to their nocturnal habits, ability of powered flight and species-specific physiological adaptations. However, knowledge of the mechanisms in place to face the variety of stressors linked with aridity is still relatively scarce, particularly concerning behaviour and in the light of the diversity characterising bats as a group.

In this thesis, I investigate further the responses and strategies that bats employ to cope with aridity, with a particular focus on the role of functional traits and movement. First, I model functional trait variation of bat assemblages to identify trends along the gradient of aridity globally. Bat assemblages inhabiting conditions of higher aridity display morphological and echolocation features more suitable to move in open habitats thanks to the greater speed and cost efficiency of flight. Additionally, larger body sizes appear to be favoured at these conditions, potentially as an advantage to reduce the exposure to cutaneous evaporative water loss by retaining a lower surface-to-volume ratio.

Despite these general trends, bat communities in arid environments still retain functional diversity, with manoeuvrable species taking benefit from their ability to hunt in the vicinity of the vegetation. Therefore, I then investigate how a low-mobility species, *Lavia frons*, copes with seasonal changes in aridity and the associated reduction in resources by following its movement using miniaturised GPS devices across a rainy and a dry season. Despite the overall low mobility observed, *L. frons* appears to respond to seasonal increases in aridity by moving over larger areas and for extended periods of time, supporting the role of movement as a strategy to offset for low prey densities during harsh periods.

Finally, due to the lack of synthesis on the topic of bat responses to aridity, I propose a narrative review integrating current available knowledge and thus providing an overview to facilitate future research. In my literature review, I cover both physiological and behavioural mechanism, pinpointing gaps in knowledge and the need of more direct studies on behaviour. Additionally, I discuss potential trade-offs among responses, focusing on the role of movement and roosting conditions in mediating the impact of environmental stressors.

This thesis brings advances in the study of bat responses to aridity, targeting some of the knowledge gaps present in the literature and setting the ground for further research. My results also highlight the importance of taking into account the interactions between physiological and behavioural mechanisms, as well as environmental conditions, when approaching the study of bat responses to aridity.

TIIVISTELMÄ

Kuivien ympäristöjen lajeja on tutkittu vähemmän kuin trooppisten alueiden lajeja. Kuivia elinympäristöjä esiintyy maapallolla kuitenkin laajalti ja siksi on tärkeää tietää miten eliöt säilyvät näillä karuilla alueilla hengissä. Lepakot elävät monenlaisissa elinympäristöissä. Osa niistä on maapallon kuivimpia, mutta niissäkin lepakot selviytyvät yöaktiivisuutensa, hyvän lentotaitonsa ja fysiologisten sopeutumiensa ansiosta. Mekanismit, etenkin käyttäytymiseen liittyvät, joiden turvin lepakot noilla alueilla selviävät tunnetaan kuitenkin melko puutteellisesti.

Tässä väitöskirjassa tutkin millaisia vasteita ja strategioita lepakoilla on kuivuuteen liittyen. Erityisenä kiinnostuksen kohteena on selvittää, mikä on toiminnallisten piirteiden ja liikkumisen merkitys. Ensin mallinnan lepakkoyhteisöjen toiminnallisten piirteiden vaihtelua selvittääkseni kuivuuden merkitystä laajassa mittakaavassa. Kuivien alueiden lepakkoyhteisöillä on sellaisia rakenteellisia ja kaikuluotaukseen liittyviä piirteitä, jotka sopivat avoimilla alueilla liikkumiseen ja saalistukseen. Näiden ansiosta niiden lento on nopeaa ja kustannustehokasta. Kuivissa oloissa valinta näyttää suosivan myös isompaa ruumiin kokoa, luultavasti siksi että se vähentää veden haihtumista.

Näistä yleisistä suuntauksista huolimatta kuivien alueiden lepakkoyhteisöjen toiminnallinen monimuotoisuus säilyy, ja kyvykkäimmät lajit hyötyvät kyvystään saalistaa kasvillisuuden lähellä. Tutkin pienien satelliittipaikantimien avulla miten vähän liikkuva *Lavia frons*-laji selviytyy kun käytettävissä olevien resurssien määrä vaihtelee kuivien ja sadekausien välillä. Heikosta liikkumiskyvystään huolimatta *L. frons* liikkui laajemmalla alueella ja pidempiä aikoja kuivina aikoina kuin sadekausina. Tällä tavalla eläimet kykenivät tavallaan kompensoimaan kuivien kausien alhaiset saalistiheydet.

Lepakoiden vasteista kuivuuteen ei tätä ennen ole tehty synteesiä. Kirjallisuuskatsauksessani käsittelen fysiologiaan ja käyttäytymiseen liittyviä mekanismeja ja tunnistan ne käyttäytymiseen liittyvät aiheet, joista tarvitaan vielä lisätutkimuksia. Lisäksi käyn läpi potentiaalisia kanssakäyntejä, keskittyen erityisesti siihen, että mikä rooli liikkumiseen ja lepopaikkoihin liittyvillä olosuhteilla on ympäristöstä johtuvien stressitekijöiden hallinnassa.

Tämä väitöskirja on edistysaskel sen selvittämisessä, että miten lepakot reagoivat kuivuuteen. Tässä tutkimuksessa on paneuduttu nykytiedoissa olleisiin aukkoihin ja samalla luotu pohjaa uusille tutkimuksille. Tulokseni korostavat, että kuivuuden vaikutuksia tutkittaessa on tärkeää huomioida fysiologisten ja käyttäytymiseen liittyvien mekanismien vuorovaikutukset ympäristötekijöitä unohtamatta.

SUMMARY

Irene Conenna

1. INTRODUCTION

1.1 ARID ENVIRONMENTS AND THEIR BAT BIODIVERSITY

Aridity is a permanent climatic feature of a region and describes the existence in the environment of a water deficit, which is determined by the imbalance between precipitation (moisture input) and evaporative demand (moisture losses) through evaporation from surfaces and transpiration from the vegetation (Pereira, Oweis, & Zairi, 2002). Aridity is therefore typically measured as the ratio between the long term means of precipitation and potential evapotranspiration (Aridity Index, AI), with values < 1 indicating a water deficit. Based on the AI, four drylands subtypes are broadly recognised: dry sub-humid (AI = 0.50–0.65), semi-arid (AI = 0.20–0.50), arid (AI = 0.05–0.20) and hyper-arid (AI < 0.05, Safriel et al., 2005). Among these, arid and hyper-arid zones are often classified together as deserts (Holzapfel, 2008; Safriel et al., 2005). In this thesis, I focus my attention (Chapters I-II) towards zones with AI < 0.5 (hereafter referred to as "arid" zones or environments, Fig. 1A), which are predominantly characterised by open-vegetation biomes (e.g. steppe, grassland, desert), while I do not directly cover ecology within dry sub-humid drylands as these regions display milder climates and a greater coverage of forest (Safriel et al., 2005). However, in Chapter I, I examine trends over the entire global aridity gradient, thus including data ranging from the humid to the hyper-arid zones.

Arid environments represent nearly 40% of the global landmass and occur on all continents, and are expected to occupy an additional 11-23% by the end of the century (Franchito, Rao, & Fernandez, 2012; Huang et al., 2016; Ward, 2016). Their primary characteristic, the scarcity of water, determines the low primary productivity observed in these regions and the progressive reduction in coverage and architectural complexity of the vegetation as aridity increases (Safriel et al., 2005; Ward, 2016). The water limitations observed in these regions have even greater impacts on the biotic component due to the strong seasonality and spatial discontinuity in rainfall patterns. In fact, precipitation comes in pulses or discrete events, determining great fluctuations in plant biomass and resource availability for the local fauna (Ward, 2016). Furthermore, abundance and temporal distribution of rain display a large between-year variability whose magnitude appears to positively correlate with degree of aridity, thus adding a component of unpredictability (Holzapfel, 2008; Safriel et al., 2005; Ward, 2016). While sharing the feature of overall aridity, arid environments differ enormously in other climatic components, such as precipitation seasonality (summer versus winter rainfall), temperature averages and daily and yearly temperature cycles (Ward, 2016). Most arid environments feature at least seasonally extremely high temperatures that exacerbate the effects of aridity. On the other hand, winter season temperatures can vary greatly across regions, with arid habitats from temperate regions, prevalently in the Northern Hemisphere, experiencing relatively or extremely cold winters. For example, average temperatures in the Great Basin, USA, range between 30°C in summer and -7°C in winter (National Park Service, 2021).

The combination of harsh conditions described above (e.g. scarcity and unpredictability of resources, extreme temperatures, etc.) represent important challenges for survival of species and impose strong selective pressures on the local fauna (Rocha, Godinho, Brito, & Nielsen, 2021; Ward, 2016). The range of adaptations displayed by arid-zone vertebrate fauna to cope with water, energy and thermal stress is extremely broad, with some strategies found across taxa while others being taxon- or species-specific (Ward, 2016). Common strategies to reduce exposure to heat and

dehydration are nocturnal activity and the use of sheltered microenvironments, e.g. underground burrows, rock crevices, etc (Holzapfel, 2008; Ward, 2016). Spatial and temporal behavioural choices are most often accompanied by physiological and morphological adaptations to conserve water. For example, comparatively low metabolic rates are found in many arid-zone birds and mammals thanks to their effectiveness in simultaneously reducing energy expenditure, heat production and consequently water loss (Schwimmer & Haim, 2009; Williams & Tieleman, 2005). In this thesis, I bring the attention towards bats. This group is of interest since it presents additional sensitivities towards aridity compared to other mammal groups, e.g. greater susceptibility to water loss (see section 1.2). Yet, bats are widely distributed and successful across a variety of arid environments (Voigt & Kingston, 2016, Fig. 1B), thanks to the development of specific behaviours and adaptations (see section 1.3), as well as to the general advantages linked to flight and nocturnality. However, our knowledge of their ecology in arid environments is still relatively scarce (see section 1.3) and advancements in this regard will likely prove important for understanding the impacts of increased global aridity in the future.

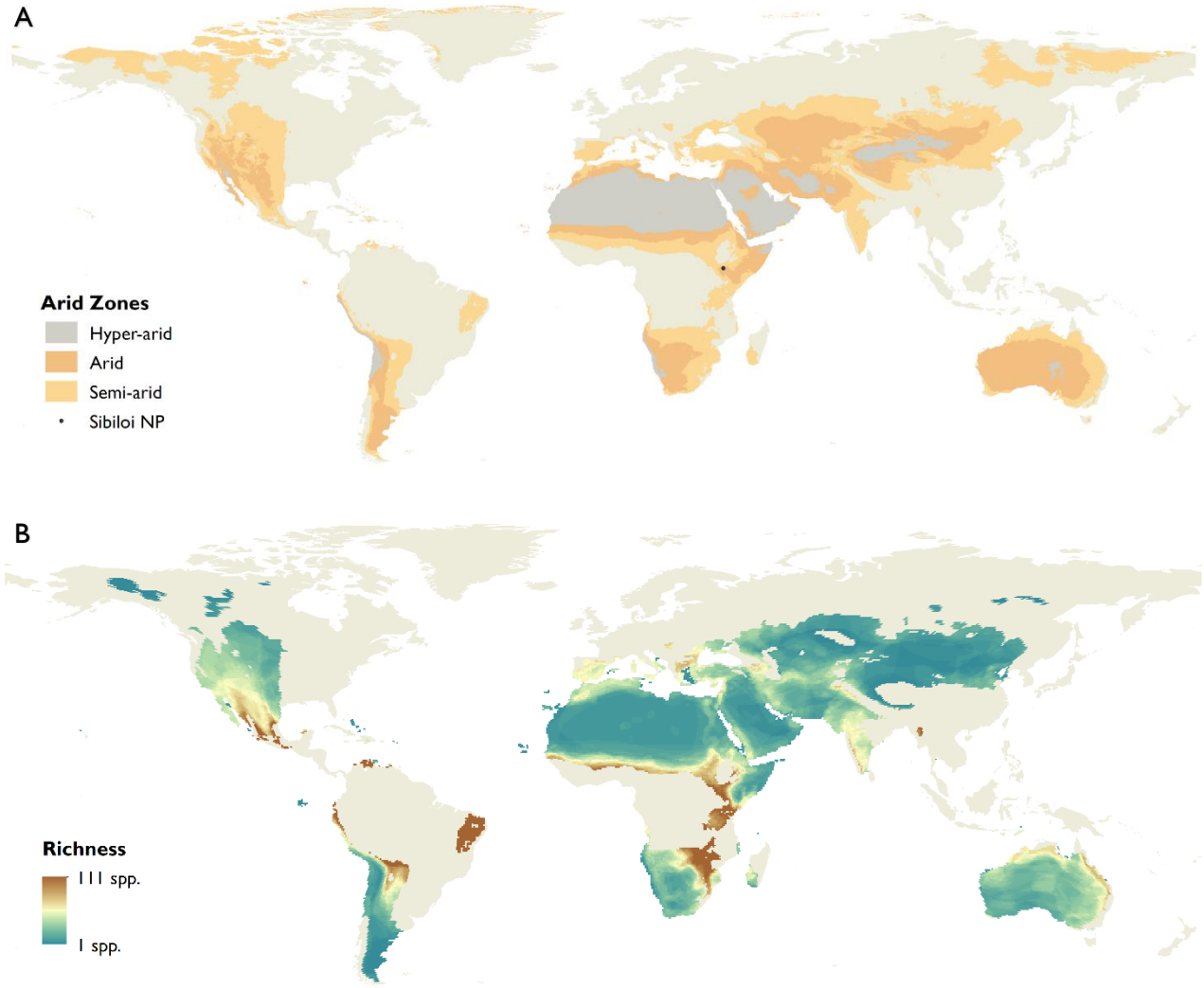

Figure 1. Maps of arid environments and their bat richness. A) Arid environments as considered in this thesis. The map is drawn based on the Aridity Index provided in (Trabucco & Zomer, 2019) and following the drylands classification illustrated in (Safriel et al., 2005). The fieldwork location of Chapter II is indicated. B) Bat richness within arid environments. Richness is calculated on a 50 km x 50 km resolution using bat range maps as provided by the Red List of Threatened Species (IUCN, 2019).

I here presents a brief overview of bat diversity in arid environments, including only species that present at least 5% of their ranges located within the specified aridity class. This was done in order to account for imprecisions in the ranges and include species for which arid environments constitute more than just a marginal component of their distributions (but see Table 1 for full overview). Of the over 1400 described species of bats (Simmons & Cirranello, 2021), over one third (n = 536) is distributed in arid environments, with a total representation of 140 genera within 16 families. However, the number of species restricted or nearly restricted to the arid climatic zone appears comparatively small (n = 88, Table 1). This trend is similarly observed in other plant and animal taxa since many species originate from the adjacent more mesic habitats (Safriel et al., 2005; Ward, 2016). Additionally, the large number of bat species (n = 267) displaying < 5% of their range in arid environments suggests that the arid zone and its climatic features represent the limit of the distribution for many species, highlighting the challenges posed by aridity on this group (Table 1). Following the general pattern of higher taxonomic diversity in areas of greater productivity, bat species richness appears to decrease with increasing aridity across the arid zone, with about 212 species extending their ranges to deserts overall and only about 59 of these being present also in hyper-arid deserts (Fig. 1B, Table 1). This is in accordance with the general trend of species richness across various animal taxa to increase as aridity declines in connection with greater environmental productivity and heterogeneity of ecosystems (Dean & Williams, 2004; Holzapfel, 2008; Safriel et al., 2005). Despite the progressive reduction in taxonomic richness, 14 bat families are still represented in deserts, with Vespertilionidae, Molossidae and Rhinolophidae being the most abundant. In my work, I focus on echolocating bats (previously also referred to as microbats, hereafter simply "bats") since these are the most abundant in the arid zone (508 out of 536) and successfully inhabit also hyper-arid deserts.

Table 1. Bat richness based on degree of exclusivity of distribution of species within arid environments overall and individual arid zones.

Aridity classes	Total spp. richness	N° spp. range > 5%	N° spp. range > 85%
Hyper-arid	196	59	2
Arid	495	207	3
Semi-arid	801	521	15
All arid zones	804	536	88

1.2 EFFECTS OF ENVIRONMENTAL ARIDITY AND ITS CORRELATES ON BATS

Bat life in arid environments is challenged in a multitude of ways. The effects exerted by aridity on bats can be both direct, linked to dehydrating conditions in conjunction with the scarcity of open water, or indirect, via the environmental correlates of aridity, e.g. low productivity and resource availability (Adams, 2010; Carpenter, 1969; Daniel, Korine, & Pinshow, 2008; Webb, Speakman, & Racey, 1995). Small body sizes in animals are associated with high evaporative water loss due to the relatively large surface-to-volume ratio (Schmidt-Nielsen, 1964; Studier, 1970). In bats, the large vascularised and uninsulated membranous wings, as well as a higher ratio of lung surface to body weight, determine an even greater exposure to cutaneous and respiratory evaporation, with rates of evaporative water loss that are twice

as high as those of similar-sized non-volant mammals (Hartman, 1963; Studier, 1970). Consequently, evaporation is the primary pathway of water loss in bats, representing up to 85% of the total water losses, and it is further enhanced by the flight activity, when wings are exposed to strong air convection (Arad & Korine, 1993; Bassett, 1980; Carpenter, 1969). In arid environments, the dehydrating conditions determine an increase in evaporation that can challenge bats particularly during day roosting, when they do not access water and temperatures in exposed roosts (e.g. tree foliage and bark, shallow rock crevices) fluctuate with the hot ambient temperatures (Maloney, Bronner, & Buffenstein, 1999; O'Farrell, Studier, & Ewing, 1971; Webb et al., 1995). In fact, at many arid locations, ambient temperatures can often approach 40°C and bats are faced with the challenge to maintain functional body temperatures while preserving water (Bondarenco, Körtner, & Geiser, 2014). Bats are then faced with the scarcity and pronounced fluctuations in both water and prey availability. While bats in seasonally cold environments are able to withstand long periods of food shortage in connection with low temperatures thanks to their ability to hibernate, in some hot semi-arid areas and deserts, climatic conditions do not permit hibernation and bats have to actively endure harsh periods. While some granivorous species, e.g. species of heteromyid rodents, can cache seeds to survive periods of food scarcity (Randall, 1993), insectivorous bats rely on insect availability, which closely follows the presence of rains and greening. During long dry seasons, cost-efficiency of the foraging activity can be greatly reduced, with many bat species relying on ephemeral resources or foraging and drinking over few permanent water sources (Adams, 2010; Egert-Berg et al., 2018; Geluso & Geluso, 2012; Korine & Pinshow, 2004; Razgour, Korine, & Saltz, 2010). Finally, broad scale changes in vegetation structure with an increased habitat openness and spacing of resources in the landscape can impact community composition based on niche selection and movement abilities of species (Denzinger & Schnitzler, 2013, see Box 1).

It is also important to consider that a greater number of bat communities will experience these conditions with the expected expansion of the arid-zone (Franchito, Rao, & Fernandez, 2012; Huang et al., 2016). Climate change will also likely impact existing arid environments, increasing frequency and duration of droughts as well as the magnitude of the stressors here described (Diffenbaugh & Field, 2013; Loarie et al., 2009). Declines in bat populations have been reported or predicted in response to warming and drying of climate (Adams, 2018; Bilgin, Kesisoglu, & Rebelo, 2012), and desert populations could be severely affected due to physiological constraints linked to life in extreme environments (Araujo et al., 2013; Rymer, Pillay, & Schradin, 2016), but research is still scarce.

1.3 BAT RESPONSES TO ARIDITY

To cope with the selective pressures described above, bats employ a variety of physiological, behavioural and morphological responses, whether in form of adaptations or plastic adjustments (Adams & Hayes, 2021; Aliperti, Kelt, Heady, & Frick, 2017; Bogan, Cryan, Weise, & Valdez, 2017). A large part of the initial as well as current research on bat adaptations to arid environments focuses on the abilities of arid-zone species to conserve water, reporting reduced rates of evaporative water loss as well as kidney specialisations to excrete highly concentrated urine (Carpenter, 1969; Geluso, 1978; Happold & Happold, 1988; Marom et al., 2006; Muñoz-Garcia et al., 2016). To cope with changes in food abundance, evidence is available showing the ability of bats to time reproduction with rainfall patterns, thus allowing for peak insect abundance when energetic demands of the young are the highest (Cumming & Bernard, 1997). In connection with the expected intensification in aridity both in arid and mesic regions, interest has increased also towards the description of behavioural mechanisms and minimal ecological requirements displayed by bats in arid environments, identifying the ability of bats to track fluctuating resources as well as the

importance of open water sources for their survival (Adams & Hayes, 2008; Adams & Hayes, 2021; Amorim, Jorge, Beja, & Rebelo, 2018; Razgour, Korine, & Saltz, 2011).

However, knowledge on bat responses to aridity is still scarce and widely scattered, particularly concerning behaviour, likely also due to difficulties in conducting field studies. While research synthesis is available for various groups of arid-zone vertebrates including small mammals (e.g. rodents: Randall, 1993; Schwimmer & Haim, 2009; ungulates: Fuller, Hetem, Maloney, & Mitchell, 2014; birds: Dean & Williams, 2004; Williams & Tieleman, 2005; reptiles: Bradshaw, 2018), bats are usually overlooked (Holzapfel, 2008; Lambers, 2018; Ward, 2016, but see Adams & Hayes, 2021). A recent review of overall research patterns on arid-zone bats by Lison et al., 2020 has highlighted how studies focus on local scales and single or few species, while community and particularly broad scale patterns have seen less coverage (but see Hackett, Korine, & Holderied, 2013; Hagen & Sabo, 2012; Hall, Lambert, Larsen, Knight, & McMillan, 2016 for examples of community ecology). Similarly, the authors identified how the topic of adaptation has received relatively scarce attention compared to e.g. taxonomy or other ecological aspects, and how certain methodologies, such as tracking and ecological modelling, have been poorly employed to study bats in these habitats (Lison et al., 2020). Finally, both effects of aridity and responses are likely to depend on the characteristics of the selected niche and the guild-specific features (see Box 1), and a greater incorporation of functional traits into studies can provide important insights into the pressures experienced by bat species and the responses implemented.

1.4 AIMS OF THIS WORK

In this PhD thesis, my overall goal has been to advance the study of bat responses to aridity. Due to the increased role that aridity will have on bat communities as a consequence of changes in climate and to the research gaps discussed above, it appears of rising importance to devote attention to the ecology of bats in arid environments. This work has two main aims: a) to generate new knowledge in the ways in which bats cope with arid conditions (I-II), and b) to unify the knowledge available in order to identify gaps and facilitate future advances in the field (III). To target these aims, I have employed a range of methodological approaches, namely modelling, field experiments and theoretical work. The thesis is composed of the following objectives:

Firstly, I focused on investigating patterns on a broad scale, to identify which functional traits features are favoured as aridity increases. Functional traits of animal assemblages have been found to respond to environmental gradients (Barnagaud et al., 2017; Holt et al., 2018), and can therefore be an asset in identifying selective pressures exerted by increasing aridity over broad geographical extents and responses of bats as a group, both of which have to date been overlooked. In Chapter I, I modelled the variation in functional trait values of bat assemblages along the global aridity gradient, hypothesising that assemblages from higher aridity areas would point to a greater ability of bats to move in open landscapes and cope with dehydration pressure.

Secondly, I assessed the species-specific responses of an arid-zone bat to seasonal increases in aridity linked to precipitation fluctuations in a desert habitat. More specifically, with Chapter II I was interested in examining changes in movement patterns between rainy and dry season in a low-mobility species (i.e. species characterised by slow and relatively energetically costly flight, see Box 1), since these species might have reduced abilities to move long distances across the landscape and therefore appear of great interest. To do so, I described both the spatial and temporal components of movement. It is unresolved how low-mobility species cope with the shortage of resources, and investigation of changes driven by

seasonality can provide new insights into the behavioural strategies used to face arid conditions.

Finally, in order to remedy the lack of synthesis in the field and promote future advancements, I undertook a review of the current knowledge available. In particular, in Chapter III I conducted a search of the literature to display the diversity of strategies and adaptations employed by bats to live in arid conditions, covering both physiological and behavioural aspects and their interplay.

2. MATERIALS AND METHODS

2.1 OVERVIEW OF METHODS

The studies included in this thesis present complementary perspectives, focusing on different taxonomic and geographical scales. Chapter I includes the largest number of bat species possible (n = 915), as allowed by data availability, and covers the aridity gradient at the global level, thus interpreting average responses irrespective of seasonal variation in aridity stress and other finer patterns. On the other hand, in Chapter II I zoom in and focus on seasonal behavioural changes of a single species at a specific location, which allows a more direct interpretation of responses, although findings are less generalizable across species. Although in Chapter I I also look at proneness to dehydration by investigating variation in body size, these first two chapters are largely dedicated to the importance of mobility and movement as strategies to deal with low resource availability. Chapter III then helps contextualise and integrate the role of movement with responses on other levels. In the following sections, I will briefly present each of the employed approaches, while detailed description of data collection and analyses are presented in the corresponding chapters. Additionally, I included informative boxes for some of the methodologies used, with the scope of providing sufficient background knowledge as well as to contextualise the techniques within the current literature.

All statistical analysis were performed in the R environment (R Core Team, 2020).

2.2 MACROECOLOGICAL APPROACH

In Chapter I, I modelled the variation of functional traits of bat assemblages along the global aridity gradient (assemblage-level analysis). Additionally, I supported the results from this main analysis by testing trends across species (species-level analysis), modelling species traits against the aridity tolerated within their ranges. This second analysis allowed incorporating phylogenetic relationships across species, and offset some of the shortcomings of the assemblage-level analysis (e.g. repeated species co-occurrence, Hawkins et al., 2017). In this project, I examined trends in wing morphology traits (aspect ratio and wing loading, Fig. 2A), echolocation (frequency of maximum energy, Fig. 2B) and body size (forearm length). Wing morphology and echolocation traits were selected in quality of good descriptors of the use of habitat by different bats (Denzinger & Schnitzler, 2013, see Box 1). Body size was chosen due to its potential for describing exposure to dehydration. Body size shows an inverse relationship with surface-to-volume ratio and cutaneous evaporative water loss, a significant pathway of water loss in bats, is a surface dependent process, thus potentially having a greater impact on smaller bats (Schmidt-Nielsen, 1964).

2.2.1 Data collection and preparation

Species trait data was collected from mammal and bat traits databases (Collen, 2012; Faurby et al., 2018; Jones et al., 2009; Wilman et al., 2014) and other published literature. I included all species of echolocating bats for which distribution data as provided by the Red List of Threatened Species (IUCN, 2019) was available, as well as the measurement for at least one functional trait of the ones considered. Due to the presence of gaps in the dataset and to the contribution of imputation in

BAT GUILDS, FUNCTIONAL TRAITS AND MOBILITY (BOX 1)

Due to the great taxonomic and ecological diversity of bats, several theoretical frameworks have been developed over time to assign bats to functional groups or guilds (i.e. a group of species that exploit the same class of environmental resources in a similar way, Root, 1967), with a recent classification proposing seven guilds (Denzinger & Schnitzler, 2013). In bats, the major constraints shaping the evolution of the sensory system and flight abilities are the relative distance between a bat in flight and the background, and the proximity of prey to the background, as these two components determine the challenge that bats have to overcome when navigating and foraging (Schnitzler, Moss, & Denzinger, 2003). Therefore, the subdivision of bats in guilds is typically based on their habitat choices and employed foraging modes (Denzinger & Schnitzler, 2013; Schnitzler et al., 2003). In this description, I focus on the presentation of the main types of foraging habitats used by bats and on the functional traits that are associated with their use, as these appear most relevant across the chapters included in this thesis.

Although definitions across the literature show some degree of variability, a consensus seem to exist in the identification of three main foraging habitats, namely open, edge and narrow space habitats (Denzinger & Schnitzler, 2013). In the open space, bats fly in unobstructed space and are not affected by the background. Open-space foragers are characterised by a fast but poorly manoeuvrable flight, and by a long-range detection of prey and background, made possible by the use of echolocation with low frequency and high source levels. On the opposite side of the spectrum, we find species foraging in the narrow space within or very close to the vegetation. These narrow-space species (also referred to in this thesis as 'low-mobility', e.g. *Lavia frons*, Fig. 2B and Chapter II) show a slow and very manoeuvrable flight, with broad and short wings, and intermediate to very high echolocation frequencies. Finally, edge-space foragers select open spaces in the vicinity of background objects and typically present intermediate characteristics (Denzinger & Schnitzler, 2013). However, it is useful to keep in mind that this is a simplification, and that species are found along a continuum between open- and narrow-space foragers features (Dietz, Dietz, & Siemers, 2006; Norberg & Rayner, 1987).

In studies involving bat functional traits, the groups here described are often identified using measures of wing morphology and echolocation (Farneda et al., 2015; Moir et al., 2021). In Chapter I, I used aspect ratio, wing loading and frequency of maximum energy (Fig. 2) as they constitute suitable proxies for wing morphology and echolocation, respectively, and are available for a great number of species. Aspect ratio (wingspan^2/wing surface) describes the shape of the wing, from narrow to broad, while wing loading (weight/wing surface) is a measure of pressure on the wings (Norberg & Rayner, 1987, Fig. 2A). Typically, bats with high values of aspect ratio and wing loading are able to cover long distances at lower energy cost than bat species with high values for these wing parameters (Norberg & Rayner, 1987). Box 1 continues in the next page.

reducing sampling bias (Nakagawa & Freckleton, 2008), I proceeded to fill in missing records via the technique 'multiple imputation by chained equation' (Van Buuren & Groothuis-Oudshoorn, 2011). To improve accuracy of imputation estimation, phylogenetic relationships among species were included in the imputation model, replicating the imputation process for 100 estimated trees to account for uncertainty in the phylogeny (Penone et al., 2014; Upham, Esselstyn, & Jetz, 2019). The imputation model included 915 echolocating bat species for which spatial data and data on at least one trait were available. Multiple imputation produces multiple datasets, in this case

In bats, functional traits have been successfully employed to study a variety of processes, e.g. from assessing impacts of environmental gradients and anthropogenic driven habitat changes at the local and regional level, to e.g. exploring sensitivity to urbanisation at the global level or understanding patterns of extinction risks across the taxon (Jones, Purvis, & Gittleman, 2003; Jung & Threlfall, 2018; Mancini et al., 2019; Moir, Richards, Rambau, & Cherry, 2021; Wordley, Sankaran, Mudappa, & Altringham, 2017). Global-level studies of functional trait variation of assemblages along environmental gradients are not yet commonly employed in bats (but see e.g. Holt et al., 2018 for trait turnover) and can offer new perspectives thanks to their potential in disclosing large-scale ecological patterns and processes (He et al., 2019; Nunes et al., 2017; Violle et al., 2014).

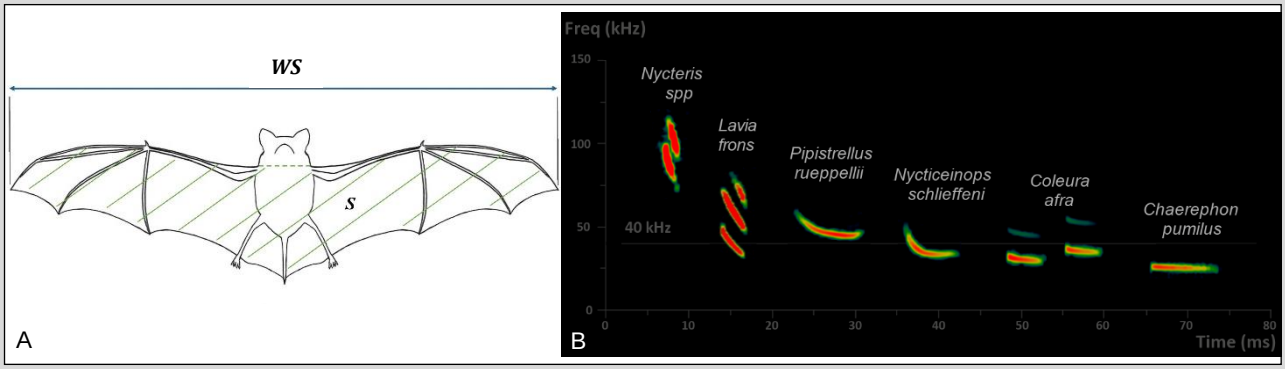

Figure 2. Wing morphology and echolocation. A) Definition of wingspan (WS) and wing surface (S) used in the estimation of aspect ratio and wing loading. B) Visual depiction of echolocation pulses as frequency (y-axis) along time (x-axis). The frequency of maximum energy (Chapter I) is the frequency at the greatest intensity of the call, depicted by a stronger red colour. The calls here illustrated are representative of some of the species found in Sibiloi National Park, Kenya, and have been measured during fieldwork activity.

set to 25 replicates, to allow for a distribution of estimates for each missing record (Cooke, Eigenbrod, & Bates, 2019). Therefore, the imputation step resulted in the generation of 2500 datasets (see Fig. 3). All datasets were retained for the analyses.

Bat assemblages were defined as species co-occurring in the same 100 km by 100 km grid cell. For each assemblage, I calculated the community weighted mean, weighted based on the proportion of the cell covered by each species, and assigned the value of aridity based on the aridity map by Trabucco & Zomer (2019). For the species-level analysis, I extracted the putative highest value of aridity within each species range.

2.2.2 Traits modelling

For the assemblage-level analysis, I utilised generalised additive models (GAMs; Wood, 2017), regarding aridity as a linear parameter and accounting for spatial autocorrelation including cell coordinates as a non-linear two-dimensional covariate. Species-level patterns were modelled using phylogenetic generalised least squares (PGLS). In both approaches, each trait was modelled independently, resulting in 10,000 models for each analysis, 2,500 for each trait. A schematic summary of the methods is illustrated in Figure 3.

2.3 FIELD-BASED APPROACH

2.3.1 The study species and study area

In Chapter II, I studied movement responses to seasonal aridity in the yellow-winged bat *Lavia frons* in Sibiloi National Park, Kenya. *L. frons* (family: Megadermatidae, Fig. 4A) is an insectivorous bat distributed roughly between 15°N and 15°S, where it is found in savannah and open woodland, often associated to riparian vegetation (Vaughan & Vaughan, 1986; Vonhof & Kalcounis, 1999). With

low values of aspect ratio and wing loading and modulated echolocation pulses (see Box 2), it is a low-mobility bat hunting in the vicinity of the vegetation with a hang-and-wait strategy (i.e. scanning the surroundings from a perch in search of prey). The area of study, Sibiloi National Park, is located in the north of Kenya along the shores of the semi-saline Lake Turkana. The climate is arid (Aridity Index ~ 0.13) and presents two rainy seasons alternating with a short and a long dry season (Avery, 2014; Mbaluka & Brown, 2016). The area is characterised by grassland and bushland vegetation, while arboreal vegetation is restricted to the riparian zone of the local ephemeral rivers (Mbaluka & Brown, 2016).

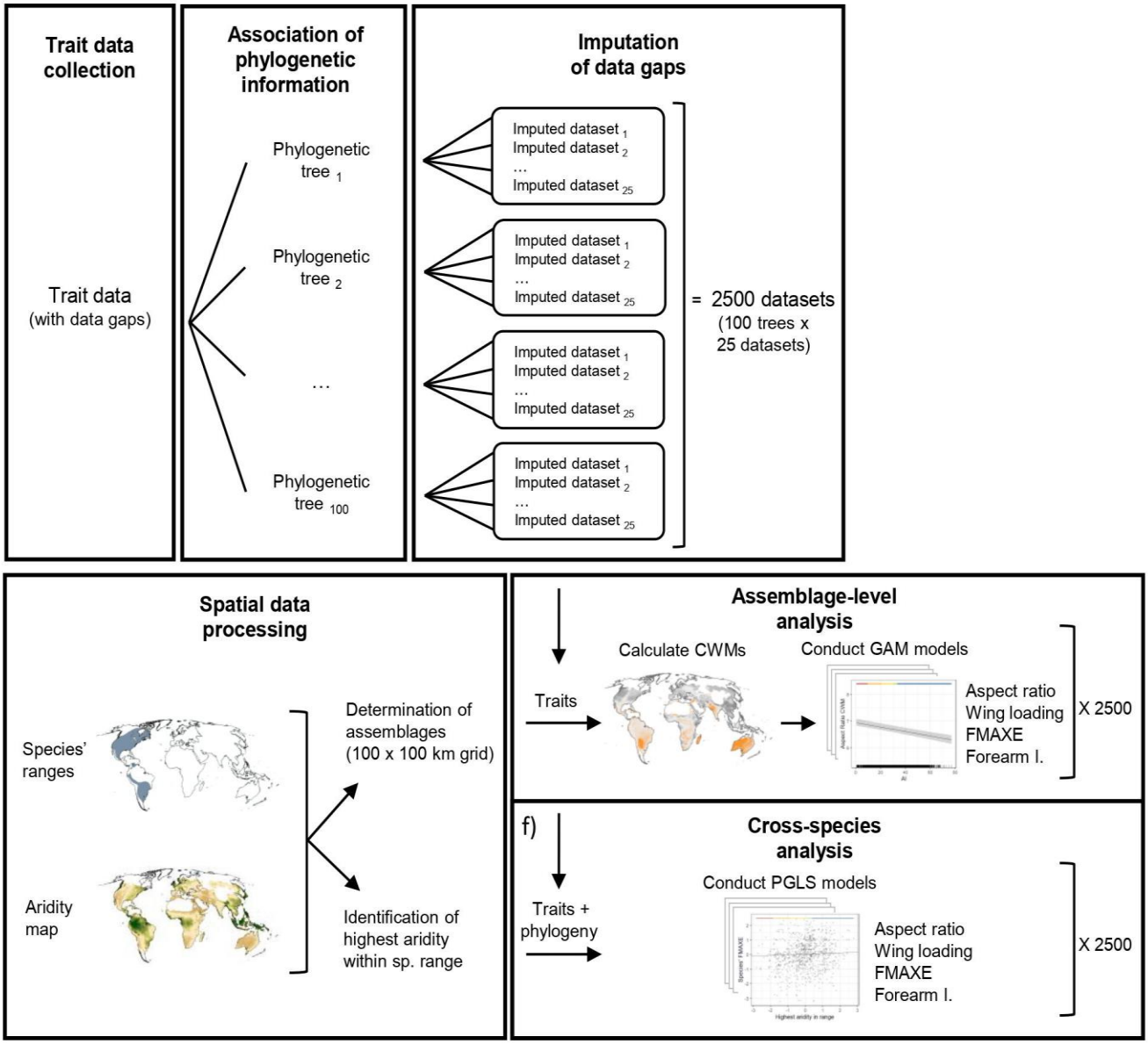

Figure 3. Methodological steps followed in Chapter I. FMAXE = frequency of maximum energy; GAM = generalized additive model; CWM = community weighted mean; PGLS = phylogenetic generalized least squares.

GPS TRACKING IN INSECTIVOROUS BATS (BOX 2)

Tracking has brought fundamental advances in the understanding of movement ecology and activity patterns in bats. However, bat small sizes and the high costs of flight have posed restrictions in employment of new devices such as GPSs (Holland & Wikelski, 2009; O'Mara, Wikelski, & Dechmann, 2014; O'Mara, Wikelski, Kranstauber, & Dechmann, 2019), reducing the benefit brought by this technology. Some of these benefits are, for example, the reduced spatial and temporal biases typical of traditional operator-based radio-tracking made possible by standardised sample regimes and improved accuracy of locations (Börger, Dalziel, & Fryxell, 2008). In addition, GPS devices allow tracking multiple individuals simultaneously and consequently the study of intra-specific interactions (Hebblewhite & Haydon, 2010). GPS loggers of weight suitable for insectivorous bats have only recently come into being and do not allow remote data download, requiring tags to be recovered after shedding from the bat.

At the onset of this thesis, GPS loggers had been employed to track insectivorous bats in merely a handful of studies (Cvikel et al., 2015; Roeleke, Blohm, Kramer-Schadt, Yovel, & Voigt, 2016; Weller et al., 2016). Over the course of this thesis work, their implementation in the study of bat ecology has significantly grown, with at least 11 studies published since 2018 (Fujioka et al., 2019; Nad'o et al., 2019; Roeleke et al., 2020; Vasenkov, Vasiliev, Sidorchuk, & Rozhnov, 2020), including the study presented here as Chapter II. However, this increase in use of GPSs has not been coupled with advancements in this technology to suit the low mass of many bat species, leading in most cases to the devices surpassing the recommended limit of 10% of the bat weight (see Table 2 in Vasenkov et al., 2020; O'Mara et al., 2014). Despite the remarkable advancements made in this field in the past three years, *Lavia frons* still is, to the best of my knowledge, the lightest insectivorous bats (15.9 - 23.7g in Chapter II) to have been tracked with GPS devices while maintaining the device weight within the 10% of the weight of the bat.

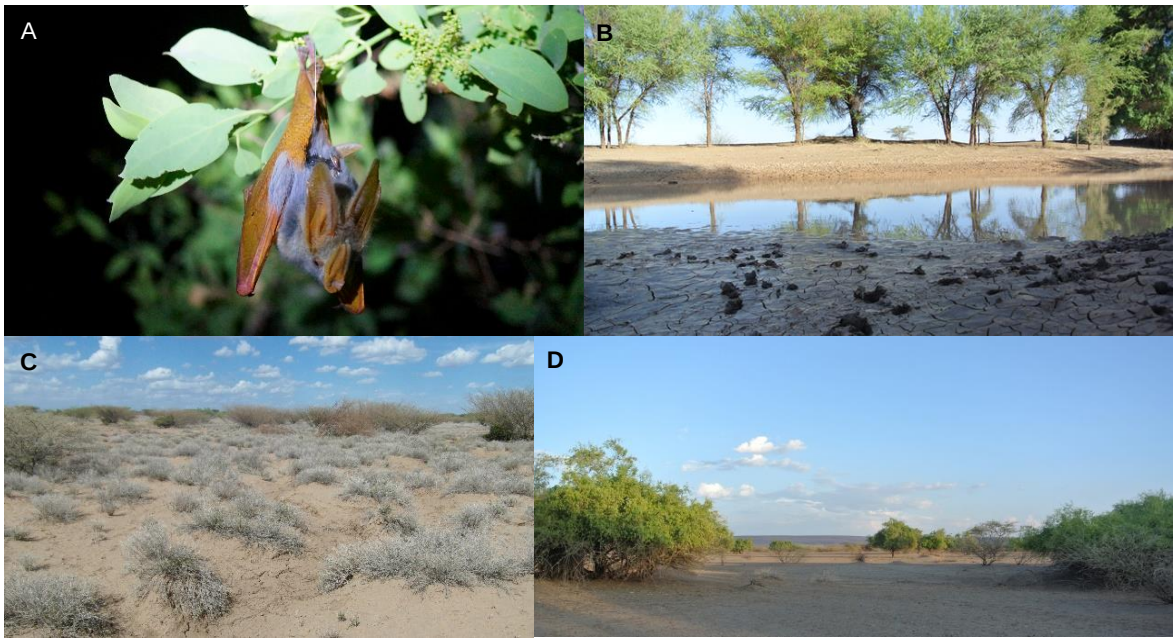

Figure 4. *Lavia frons* and field site. A) *L. frons* hanging from a branch of *Salvadora persica* and carrying a GPS device; B) one of the field locations in a riverbed in Sibiloi National Park, Kenya, during the rainy season; C-D) habitats surrounding the river at the tracking locations during the dry season. Credits for B and D: Joni Uusitalo.

2.3.2 Field sampling and statistical analyses

Tracking took place during the rainy season (April-May) in 2017 and during the short dry season (January-February) in 2018. Bats were captured at four locations along a dry but vegetated river (Fig. 4) and at increasing distance from the lake, and were equipped with rechargeable 1g GPS loggers (see Box 2). Since these GPS trackers lacked the possibility of remote download of the data due to the limited battery capacity, they were deployed in association with light VHF transmitters, which allowed tag retrieval after tracking. The tracking schedule was established to record bat location between 18:00 in the evening and 5:30 in the morning for seven consecutive nights, and, when possible, bats from the same site were tracked simultaneously to allow description of movements in relation to neighbouring individuals. Altogether, 22 bats out of 29 were successfully tracked, 13 during the rainy season and 9 during the dry season, for a total of 1802 locations recorded. To investigate seasonal variation in the spatial component of movement, I estimated home ranges and core areas used by bats, and evaluated potential differences between the two seasons. Home ranges and core areas were estimated by measuring the area delimited by the 95% and 50% levels, respectively, of the kernel density estimations defined by their recorded locations. To assess changes in the temporal component of movement, I quantified bat temporal activity as the minimum distance travelled per hour. While this measure of covered distance likely underestimates actual movements, it represents a suitable proxy for activity in a species displaying a hang-and-wait hunting behaviour. With this data on movement activity patterns across the night, I first identified the high and low activity peaks within each season, and then tested differences between the two seasons using linear mixed-effects models for both analyses.

2.4 THEORETICAL APPROACH

In Chapter III, I conducted a narrative review to display the diversity of bat responses to aridity. I performed a literature search between November 2020 and January 2021 using the following search string: (bat$ OR chiroptera) AND (dryland$ OR "semi-arid" OR semiarid OR arid* OR desert* OR "hyper-arid" OR hyperarid OR xeric). Papers were retrieved from Web of Science without restriction on publication years. Additionally, I also examined the first 300 records from Google Scholar and integrated these outputs by including relevant publications encountered during the reading phase, as well as from authors' personal databases. A semi-systematic search style to collect publications was chosen to allow expanding the pool of publications considered for review. I chose to include in the search string terms pointing to general publications on bats in arid areas, without further restricting the topic, as this permitted to retrieve also studies dealing with responses to aridity indirectly. Studies selected for review dealt, both directly and indirectly, with strategies and adaptations to aridity and had study sites located in the arid zone. Reproductive strategies and importance of water for bats in these environments were not covered in this review, but are otherwise summarised in other publications (see e.g. Adams & Hayes, 2021).

3. RESULTS AND DISCUSSION

In this discussion, I will present my findings focusing on the integrative results across the three chapters based on topics covered. Further discussion on the specific aspects covered by each study can be found in the corresponding chapters.

3.1 MOVEMENT AS A RESPONSE TO ARIDITY

My results reveal the use by bats of various forms of movement as a response to aridity at different levels. Indeed, movement strategies have been shown to be an important part of the set of adaptations to aridity in a number of taxa (Dean & Williams, 2004; Randall, 1993). For example, most deserts birds display some degree of

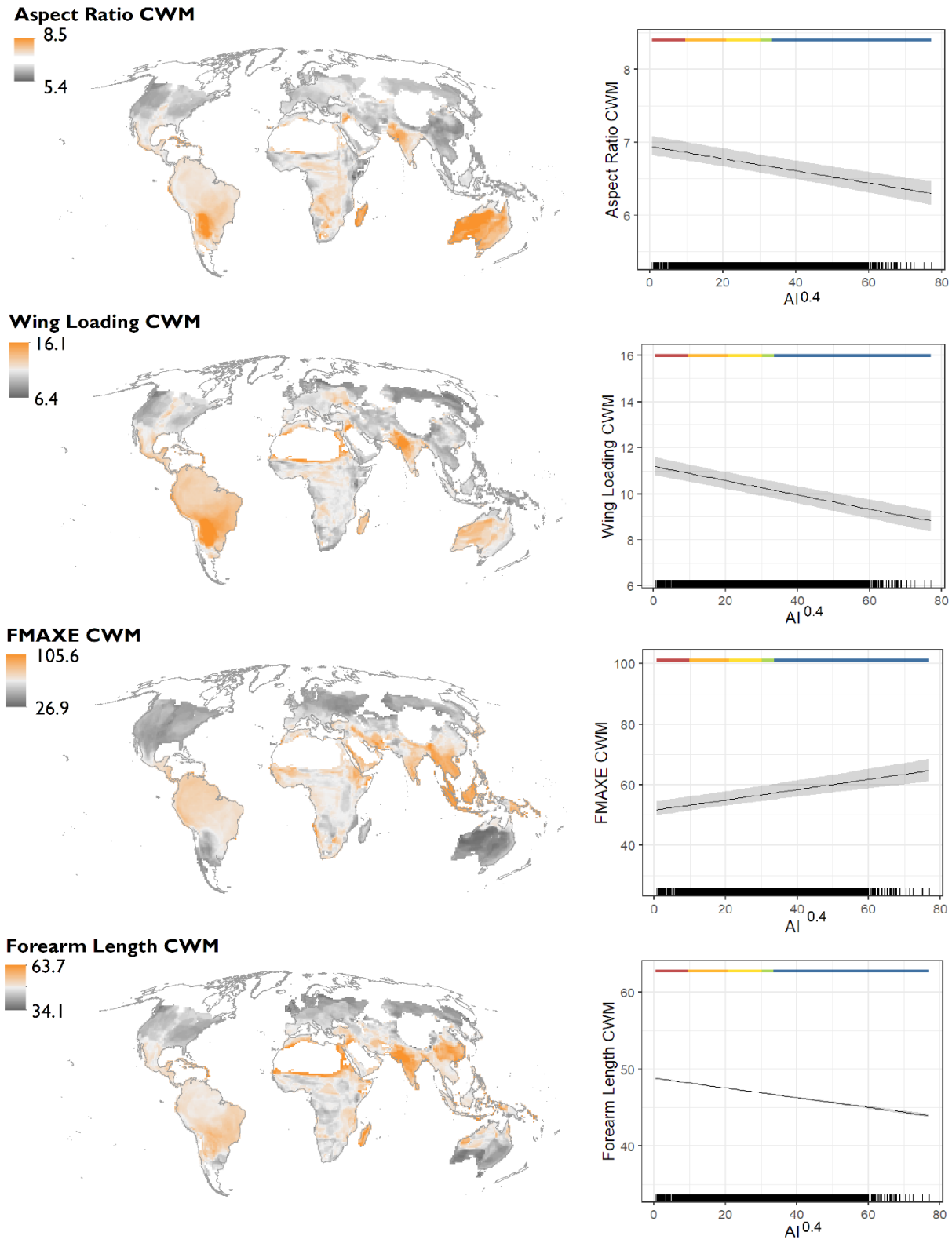

Figure 5. Functional traits variation along the global aridity gradient. Left panels: geographical distributions of community weighted means (CWMs) for the traits considered in Chapter I. Right panels: graphs illustrating the variation of trait CWMs of assemblages along the aridity gradient and model uncertainty (shaded area), across the 2,500 models per trait, derived from data imputation. Lower values of the Aridity Index (AI) correspond to higher aridity levels as signalled by the colour bar. FMAXE = frequency of maximum energy.

nomadism, whether locally or over large distances, as a way to cope with the unpredictability of arid ecosystems (Dean & Williams, 2004).

In Chapter I, I looked at the variation along the aridity gradient of morphological traits describing habitat associations as well as overall movement abilities in bats. I detected an increase in bat assemblage values of wing aspect ratio and loading, accompanied by a decrease in echolocation frequency, along the gradient from humid to hyper-arid environments, supporting my hypothesis that species inhabiting arid areas would appear better equipped to move and forage in structurally more open spaces (Fig. 5). While these trends can be an outcome of the lack of selective pressures linked with flight in cluttered environments, it is also possible for these features to be actively selected due to the advantages that are associated with greater movement abilities in coping with low density of resources in the landscape. These could include e.g. allowing species to track water availability, locate ephemeral patches of prey or covering large distances between roosting sites and foraging grounds. High values of aspect ratio and wing loading would facilitate long-range movements and quick responses to insect concentrations by providing, respectively, greater cost-efficiency and speed of flight (Norberg & Rayner, 1987). For example, nectarivorous bats have been shown to carry out round trips of up to 104 km to commute between roosting and foraging sites nightly (Goldshtein et al., 2020; Medellin et al., 2018, Chapter III). Similarly, the open-space insectivorous bat *Rhinopoma microphyllum* visits a large number of sites every night searching for insect swarms (Egert-Berg et al., 2018, Chapter III).

However, these patterns constitute general global trends, and species foraging close to the vegetation and presenting relatively low values for wing parameters and high echolocation frequencies still persist at high aridity, likely thanks to their ability to hunt prey closely associated to the vegetation, both on the wings and by gleaning arthropods from leaves and ground (Bell, 1982; Korine & Pinshow, 2004). It appears therefore of great interest to investigate the role that movement holds in these species in coping with seasonal drops in resources.

To provide insights into this topic, in Chapter II I followed the movements of *L. frons*, a low-mobility species, across the rainy and dry season in a desert. Overall, the individuals of *L. frons* tracked in this study showed a strong site fidelity and some of the smallest home range sizes recorded for bats (Fig. 6). Despite this peculiarity, this species appeared to respond to increases in aridity by covering larger areas during the dry season (i.e. enlarging its home ranges). Changes in the spatial component of movement are associated with significant variations in the temporal component of movement. In particular, while in the rainy season movement activity decreased soon after an evening activity peak, during the dry season it persisted throughout the whole night, with just a minor drop between 01:00 and 02:00 (Fig. 7). These seasonal variations in movement patterns could be a response to the lower prey availability, determining the need for the bats to visit additional locations and increase activity levels in order to ensure sufficient foraging success. This strategy supports the role of movement in offsetting for food shortages during dry periods, even in species relying on short-range movements. Enlarged home ranges in response to drought have also been hypothesised for *Tadarida brasiliensis* in New Mexico (Best & Geluso, 2003, Chapter III). However, studies addressing directly seasonal changes are scarce also due to obstacles in implementing field tracking of bats across seasons.

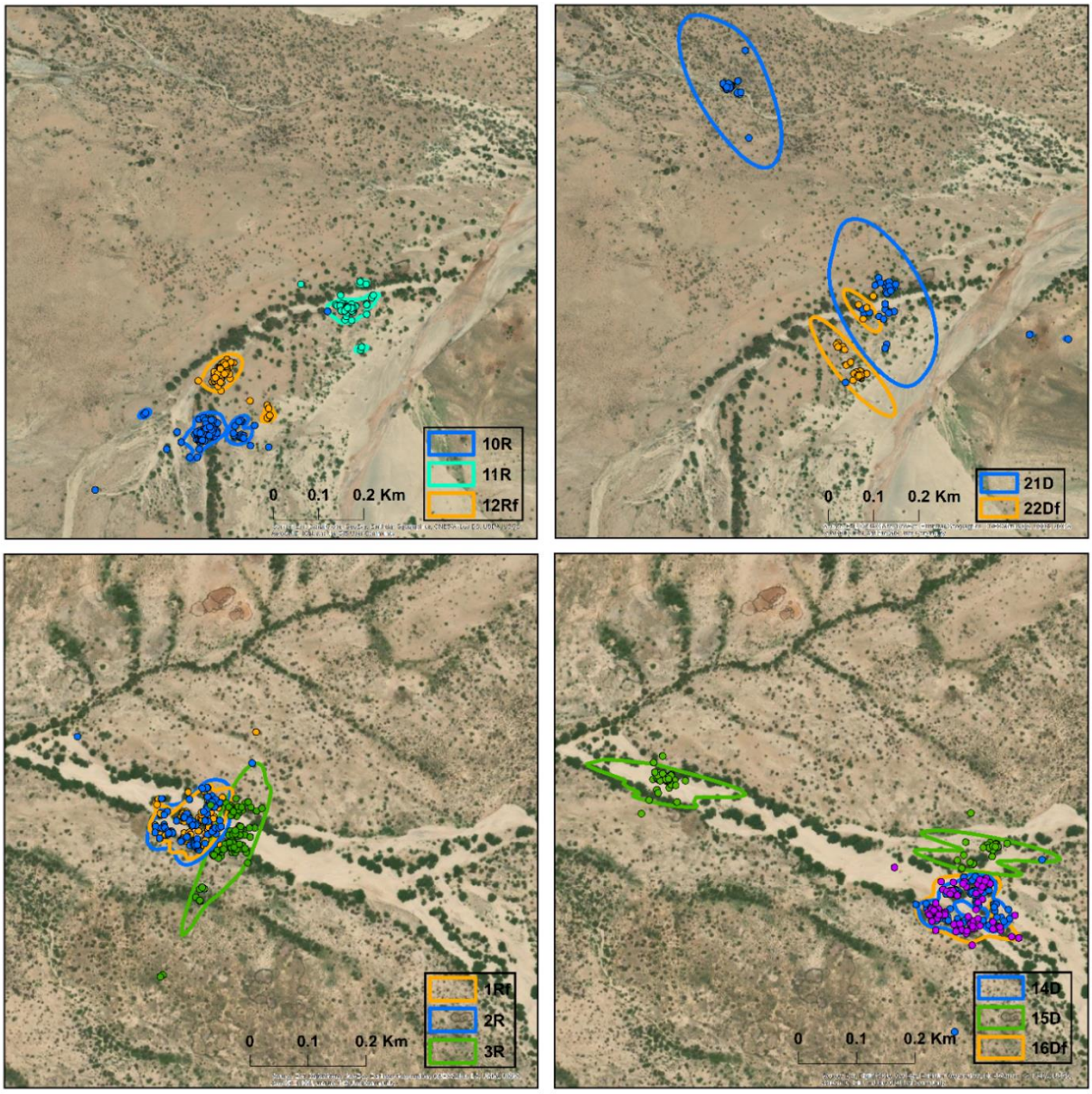

Figure 6. Home ranges in *L. frons*. The left panels show home ranges for a sample of the individuals tracked in Chapter II during the rainy season, while the right panels show home ranges at the same locations during the dry seasons. Each number identifies a different individual. The location depicted in the top panels is the closest to Lake Turkana (< 2km).

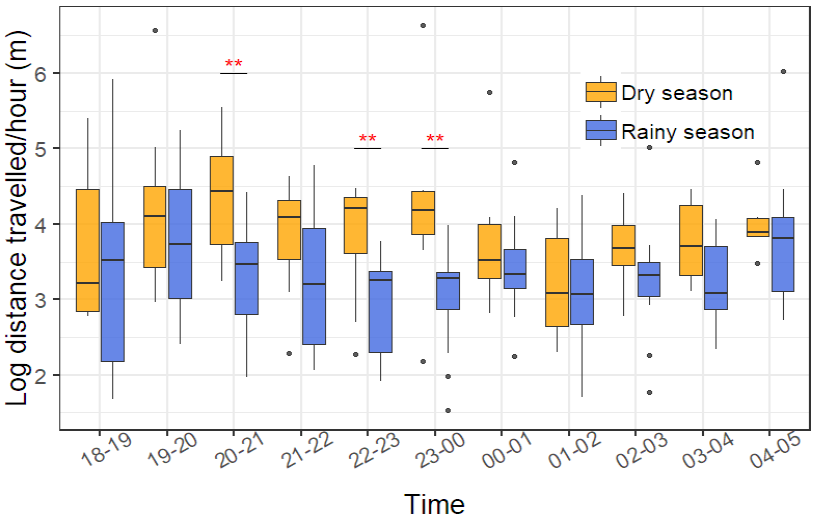

Figure 7. Seasonal differences in movement partitioning across the night. Each value represents the average log-minimum distance travelled/hour per bat at each time interval. Asterisks indicate significant differences between the two seasons for a certain time interval.

On the other hand, increased movements might reduce cost-efficiency of foraging, particularly in slow fliers, and trade-offs might exists, with sublethal costs of behavioural compensations likely reducing overall fitness (Cunningham, Gardner, & Martin, 2021; Speakman, Thomas, Kunz, & Fenton, 2005). Additionally, the bats were tracked during a short dry season (January-February 2018) after a period of above-average precipitation (i.e. short rainy season of October-December 2017 with between 140 and 200 percent of normal precipitations; Kenya Food Security Steering Group, 2018). Occurrence of La Niña events determines drier conditions in equatorial East Africa including Kenya (Holmgren et al., 2001), and I would expect that effects of aridity during a long dry season as well as years of drought would show to be more pronounced. On the other hand, *L. frons* did not show movements dedicated to the access to freestanding water, which during the dry season is represented only by the semi-saline lake (usually located > 10 km away from the bats). Such long commutes would probably exert excessive energy as well as evaporative stresses on this species. Further discussion on potential mechanisms to deal with water stress in *L. frons* is presented in the next section.

In addition to the movement strategies presented above, some species also employ various degrees of migratory behaviour, from short-distance, to regional as well as long-distance (Chapter III). This type of response is observed, for example, in desert-dwelling species of nectarivorous bats, which rely on the nectar and fruit provided by cacti and agave (Bogan et al., 2017; Fleming & Holland, 2018; Rojas-Martinez et al., 1999). Nectarivorous bats present adapted physiology to feed on high water-content food and their water requirements cannot be met in absence of these resources, thus determining the migratory behaviour (Carpenter, 1969). Similarly, species of insectivorous bats have been shown to migrate or show shifts in ranges to follow favourable precipitation conditions (Bullen & McKenzie, 2005; O'Shea & Vaughan, 1980; Villa & Cockrum, 1962).

3.2 OTHER MECHANISMS TO COPE WITH DEHYDRATION PRESSURE AND WATER SCARCITY

In addition to the range of movement responses to ensure access to water listed above, bats display a variety of other strategies to deal with water stress. In Chapter I, I aimed to investigate the trend of body size in bat assemblages along the aridity gradient, hypothesising a role of this trait in mediating exposure to dehydration due to the dependence of cutaneous evaporative water loss rate on body surface. My results depicted an increase in body size with aridity (Fig. 5), which I interpreted as a morphological mechanism providing an advantage in reducing exposure to water loss. While this relationship had not been previously investigated for bats, this positive association between body size and aridity is not unprecedented and has already been theorised in James (1970) and Nevo (1973) ("water conservation hypothesis") and more recently identified in anurans in the Neotropical Cerrado ("water availability hypothesis", Olalla-Tárraga, Diniz, Bastos, & Rodríguez, 2009). Additionally, in Chapter I, the increase in wing loading (i.e. a measure of body size relative to wing surface) at greater aridity also identifies a reduction of wing surface relative to body size and therefore an overall smaller exposed surface.

In Chapter III, I then provide a review of the physiological and behavioural adaptations present in the literature. Evidence is available showing lower rates of cutaneous evaporative water loss in desert bat species in a normothermic state compared to species inhabiting mesic area, although the mechanisms driving these changes are still not fully understood (Marom et al., 2006; Muñoz-Garcia et al., 2016). In other taxa of mammals and birds such adaptation has been related with a structure of the stratum corneum of the epidermis specialised to promote water conservation (Haugen, Williams, Wertz, & Tieleman, 2003; Muñoz-Garcia, Ro, Brown, & Williams, 2008; Muñoz-Garcia & Williams, 2005), but information for bats is still

limited (Muñoz-Garcia, Ro, Reichard, Kunz, & Williams, 2012). Suggestions have been made about a possible role of reduced capillarisation of the wing membranes to reduce evaporation through the skin (Vogel, 1969). Evaporative water loss is also efficiently reduced by bats during torpor and hibernation in connection with lowered metabolic rates, and some species select roosting sites that effectively buffer them from outside conditions and provide favourable humidity levels (Czenze, Naidoo, Kotze, & McKechnie, 2020; Muñoz-Garcia et al., 2016; Stawski, Willis, & Geiser, 2014; Toussaint & McKechnie, 2012). Finally, several desert-dwelling bat species are equipped with specialised kidneys that allow them to conserve water by producing hyperosmotic urine (Bassett, 1986; Carpenter, 1969; Geluso, 1978; Happold & Happold, 1988). Many bat species inhabiting the arid zone present wide distributions spanning across arid and mesic regions, and some of the responses listed above have been found to be featured only in the arid portion of their ranges (Bassett, 1982; Gearhart, Adams, Pinshow, & Korine, 2020), pointing at the importance of intraspecific behavioural and physiological plasticity and local adaptation. The topic of intraspecific variation in responses, to date scarcely explored, would deserve more attention due to the potential importance of trait flexibility for species to successfully adjust to upcoming environmental changes (Rymer et al., 2016).

Despite the multitude of strategies displayed by bats to reduce water loss, no study provides direct evidence of independence of insectivorous bats from drinking under natural conditions (but see e.g. Geluso, 1978; Happold & Happold, 1988 for laboratory studies and Roer, 1970 for semi-natural conditions; Chapter III). This possibility has been considered for some desert-adapted species and some indirect evidence (e.g. failure to observe certain species drinking over extended field studies) is available (Carpenter, 1969; Korine & Pinshow, 2004; Razgour et al., 2010; Roer, 1970). As previously mentioned, in Chapter II I did not detect movements in *L. frons* to access open water. Due to the low sampling frequency of our GPSs (every 30 or 60 minutes), it is not possible to determine the habits of the species during the rainy season, when pools of water might be available at several locations along the river. However, during the dry seasons the only open water sources are the semi-saline lake and few artificial watering points that are located at large distances from most of the bats home ranges. Therefore, regular excursions to such features would have likely been recorded had they occurred, and the data allows speculating independence of this species from drinking during the dry season. While dehydration stress can be particularly high in these conditions, during this period the bats are not burdened by the extra water requirements linked to lactation, which has been shown to determine significantly higher rates of drinking in female bats due to the high water content of milk (Adams & Hayes, 2008; Kunzet al. 1995). These observations could therefore add to the indirect evidence supporting the possibility of some degree of independence of bats from water in arid environments. While *L. frons* successfully inhabits arid environments (~37%), it is only marginally present in deserts (~7.5%). If *L. frons* relied on insects for its water intake during dry seasons, the threshold in tolerance of aridity in this species could be associated with the extreme challenges faced in locating food resources, in concert with limited movement abilities and high flight costs.

3.3 ROLES OF CO-OCCURRING ENVIRONMENTAL VARIABLES AND INTERACTION OF RESPONSES

The specific responses to aridity presented by each species are influenced by a variety of factors, the first of which is the set of environmental variables accompanying aridity in a certain region, e.g. temperature, seasonality patterns, degree of unpredictability. For example, in regions with cold winters bats have the chance to employ hibernation to endure the winter period (O'Farrell & Bradley, 1977). In warm areas instead, it has been shown that some species have adapted to enter torpor at

higher temperatures to be able to benefit from the advantages of increased water and energy conservation (Bondarenco, Körtner, & Geiser, 2013; Marom et al., 2006).

Alongside the importance of co-occurring climatic conditions in driving responses to aridity, interactions and trade-offs among these responses could exist. Particularly, roosting habits and movement abilities could hold a role in shaping the set of conditions and the degree of stress experienced by each individual species. Roosting habits define the levels of temperature and humidity the species are exposed to during the daytime when access to resources is not possible (Bassett, 1986; Czenze et al., 2020). Therefore, responses on other levels, e.g. physiology, could be to some extent complementary. For example, Toussaint & McKechnie (2012) measured relatively high evaporative water loss rates and low heat tolerance in an arid-zone species, *Nycteris thebaica*, choosing well-buffered baobab tree cavities as roosting sites (Chapter III). On the other hand, some species roosting in exposed conditions, such as *Scotorepens greyii*, have been shown to tolerate high ambient temperatures, choosing to thermoconform rather than thermoregulate, likely to save water, even at body temperatures above their thermoneutral zone (Bondarenco et al., 2014, Chapter III). Species roosting in these conditions might also take greater advantage of torpor bouts by following fluctuating ambient temperatures and employing passive arousal from torpor to save energy and water (Bondarenco, Körtner, & Geiser, 2016; Korine, Daniel, & Pinshow, 2013; Schorr & Siemers, 2013).

Similarly, movement abilities determine bat possibilities and costs to successfully access resources at night-time. Mobile bats can e.g. track water availability by switching from temporary to permanent water sources seasonally, thus also counting on a more stable source of food (Geluso & Geluso, 2012; Razgour et al., 2011). On the other hand, low-mobility bats such as *L. frons* during dry seasons will be more tightly linked to local resource availability (Chapter II). However, to the best of my knowledge, no information on physiological responses is available for this species. Similar interactions have been identified in other taxa as well, e.g. in heteromyd rodents, for which movement abilities and costs can determine whether a species will be more likely to travel to another site to locate food, or rather cope with local conditions (Randall, 1993). Further interactions between responses to aridity other than the ones here presented are likely to exist, with influencing factors being species- and location- specific. From the knowledge gathered in Chapter III, it appears therefore important to jointly consider, in addition to local environmental conditions, physiological and behavioural adaptations and their interactions in defining the ability of a species to persist in arid environments.

4. CONCLUSIONS

The goal of this thesis work was to advance the study of responses of bats to environmental aridity by addressing some of the gaps present in the literature and unifying the knowledge available.

Overall, the results from my original studies identify movement as a fundamental component of the set of strategies employed to cope with aridity. At the global scale, this is signalled by the increase in movement abilities of bat assemblages as the climate becomes more arid. The advantage of fast and efficient flight in arid environments is likely due to the greater availability of open space, as well as to the need to locate scattered resources. This trend could be determined by either a relative increase in proportion in the community of species with greater mobility, or to an overall variation in mobility across guilds, or a combination of the two. Nevertheless, this trend constitutes a generalisation, and arid-zone bat communities still retain a diversity of narrow-space foragers. The data obtained showed that movement strategies represent an important asset even in these low-mobility species, despite deviations from preferred

movement patterns in these species might come at high energetic costs and trade-offs. *L. frons* appeared to respond to the seasonally higher aridity by increasing movement and foraging efforts, likely as a way to compensate for lower prey densities. However, *L. frons* has a high roosting and foraging site fidelity and is peculiar in the extremely small extent of its movements and it remains to be investigated whether other species of narrow-space foragers might show analogous patterns.

Interestingly, my results also suggest a potential benefit of larger body sizes in arid conditions, which I explained as a mechanisms to lower evaporative water loss pressure. While previously described for other taxa, this trend has yet received little attention in bats. We do not know whether such variation in body size exists also at the intraspecific level across mesic and arid portion of species ranges, or how other climatic factors, e.g. temperature, can interact with aridity in determining broad scale trends in body size. Overall, a greater number of studies targeting intraspecific variations across species distributions or seasons can be particularly useful to bring new insights into behavioural, morphological and physiological strategies by looking at plasticity and local adaptations.

Finally, the integration of the empirical and theoretical studies allowed identifying the importance of considering the interaction among responses, since trade-offs are likely to exist between physiological, morphological and behavioural mechanisms. It would be of interest for future efforts to evaluate whether bats could be subdivided in few groups based on similarity in strategies to cope with aridity or whether more clear links can be established across behavioural and physiological traits. For example, mobile bats utilising buffered roosts could show less specialised physiological adaptations, in opposition to desert-adapted low-mobility species that would rely primarily on physiological adaptations. With the results of this thesis, a tentative interpretation can be made only for the case of *L. frons*. Given the observed low mobility of this species and apparent low dependency on water sources during the dry season, *L. frons* might present physiological features to conserve water sufficient to be able to rely primarily on food rather than water intake, at least seasonally. However, sufficient food abundance even in the harshest periods of the year might be required to avoid unsustainable foraging costs, thus preventing this species from occupying the most arid environments, as indicated by its limited range extension within deserts. Future studies employing a similar integrative view of strategies could bring fundamental advances in the understanding of bat ecology in arid environments.

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